

University of Groningen

Paternal care and male mate-attraction effort in the European starling is adjusted to clutch size

Komdeur, J.; Wiersma, P.; Magrath, M.

Published in:

Proceedings of the Royal Society of London. Series B, Biological Sciences

DOI:

[10.1098/rspb.2002.1987](https://doi.org/10.1098/rspb.2002.1987)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2002

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Komdeur, J., Wiersma, P., & Magrath, M. (2002). Paternal care and male mate-attraction effort in the European starling is adjusted to clutch size. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 269(1497), 1253-1261. <https://doi.org/10.1098/rspb.2002.1987>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Paternal care and male mate-attraction effort in the European starling is adjusted to clutch size

Jan Komdeur^{1*}, Popko Wiersma¹ and Michael Magrath^{1,2}

¹*Zoological Laboratory, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*

²*Department of Zoology, University of Melbourne, Parkville, VA 3052, Australia*

In facultative polygynous birds with biparental care, a trade-off may occur between male parental care and attraction of additional mates. If there is a cost associated with reduced male parental care, the relative benefit of mate attraction may be predicted to decrease as the size of a male's clutch or brood increases. We tested this prediction in monogamous pairs of facultatively polygynous European starlings (*Sturnus vulgaris*). The larger the clutch, the more time the male spent incubating and the less time he spent attracting an additional female (i.e. singing near and carrying green nesting material into adjacent empty nest-boxes). Reduced paternal incubation resulted in lower overall incubation (the female did not compensate) and lower hatching success. Immediately after experimental reduction of clutches, males spent significantly less time incubating and more time singing and carrying greenery, and vice versa for experimentally enlarged clutches. Males with experimentally reduced clutches attracted a second female more often than males with experimentally enlarged clutches. This is the first study, to our knowledge, to provide experimental evidence for an adjustment of paternal care and male mate-attraction effort to clutch size. However, a trade-off between paternal nestling provisioning and mate attraction was not revealed, probably due to the absence of unpaired females by that time in the breeding season. Experiments showed that the relative contribution of the male and female to nestling provisioning was unrelated to brood size.

Keywords: parental care; incubation; clutch size; food provisioning; brood size; reproductive trade-off

1. INTRODUCTION

Males of many bird species contribute to one or more aspects of parental care, such as incubation of eggs and feeding of the young (Clutton-Brock 1991). In many of these species, males also seek additional mates (Yasukawa & Searcy 1982; Hannon 1984; Breiehagen & Slagsvold 1988; Dunn & Hannon 1991; Veiga 1992; Kempenaers 1994; Slagsvold & Lifjeld 1994; Sandell & Smith 1996) or copulations with females other than their social mate (extra-pair copulations; EPCs), which can result in extra-pair fertilizations (EPFs) (Birkhead *et al.* 1990; Gibbs *et al.* 1990; Birkhead & Møller 1992; Kempenaers *et al.* 1992; Dixon *et al.* 1994; Westneat & Webster 1994; Wetton *et al.* 1995). Currently, there is considerable interest in the consequences of mating status and EPFs for the amount of parental care provided. Most research has focused on paternal care in relation either to a change in mating status (Orians 1969; Searcy & Yasukawa 1989; Slagsvold & Lifjeld 1994; Bruun *et al.* 1997; Smith & Sandell 1998), or to a perceived loss of paternity in their nest (Whittingham *et al.* 1992; Westneat & Sherman 1993; Westneat & Sargent 1996). However, the amount of care provided by the male may also vary inversely in relation to his opportunities to attract additional mates (Emlen & Oring 1977) or EPCs (Trivers 1972; Maynard Smith 1978; Beecher & Beecher 1979; Patterson *et al.* 1980; Westneat *et al.* 1990). So far, this latter prediction has received less attention (Whittingham 1993; Smith 1995; Cucco & Malacarne 1997; Magrath &

Elgar 1997; Smith & Härdling 2000). One factor that may affect the benefits of paternal care is clutch or brood size. Males attending large clutches (broods) may have relatively less to gain from pursuing EPCs or attracting additional mates than males with small clutches (broods) (Westneat 1988; Westneat *et al.* 1990; Wright & Cuthill 1990; Whittingham 1993; Magrath & Elgar 1997; Smith & Härdling 2000). Consequently, the size of the clutch or brood may influence the conflict between paternal care and mate attraction. Given that males, compared with females, typically have greater opportunities for increasing their reproductive success through EPCs or by attracting additional mates and may therefore pay a higher cost in terms of lost fitness by providing care, additional eggs in a clutch should be of greater value to males than females (Smith & Härdling 2000). The only empirical support for a clutch-size-related response comes from a study on fairy martins (*Hirundo ariel*), in which males with smaller than average clutches contributed less to incubation and were more responsive to the proportion of fertile females in colonies than males with larger clutches (Magrath & Elgar 1997). Until now, there has been no experimental support for the effects of clutch or brood size on male participation in parental care on the one hand, and mate attraction, or extra-pair mating effort, on the other hand (Webster 1991; Smith 1995; Magrath & Elgar 1997; Smith & Härdling 2000). In this study on the European starling (*Sturnus vulgaris*), we test experimentally for the existence of such a trade-off.

The facultatively polygynous European starling is a semi-colonially breeding, hole-nesting passerine. Starlings have communal feeding areas and males defend only the nest hole, not the food resource (Feare 1984). Monog-

* Author for correspondence (j.komdeur@biol.rug.nl).

amous males contribute substantially to both incubation and feeding of the young and provide significantly more care than polygynous males (Pinxten & Eens 1994; Smith *et al.* 1995; Sandell *et al.* 1996). EPCs occur with already-mated females, usually neighbours (Eens & Pinxten 1990; Pinxten *et al.* 1993; Smith & Von Schantz 1993; Pinxten & Eens 1994). Males engaging in extra-pair courtship approach non-mate females very closely (usually high up in trees) and then start singing to invite copulation (Eens & Pinxten 1990; Pinxten & Eens 1997). Conversely, paired males trying to attract an additional mate must first occupy an additional nest-box. They usually sing very close to or in this nest-box using 'wing-waving' displays (Feare 1984; Eens & Pinxten 1990; L. Brouwer and J. Komdeur, personal communication) and carry green nesting materials into the nest-box when females are in close proximity to the nest-box (Eens *et al.* 1993; Gwinner 1997; L. Brouwer and J. Komdeur, personal communication). The frequency of male singing close to an empty nest-box during incubation of the first clutch is positively associated with the acquisition of a secondary mate (Merkel 1978; Cuthill & Hindmarsh 1985; Eens *et al.* 1990, 1991; Mountjoy & Lemon 1991; Smith 1995; Pinxten & Eens 1998; this study). We considered only breeding pairs that were monogamous before the onset of clutch and brood-size manipulations and that had one empty nest-box within 2 m of their own nest-box (i.e. within the territory already defended by the male; Smith (1995)). This study was designed to answer four questions: (i) does clutch or brood size affect the amount of parental care?; (ii) what are the benefits of paternal care in terms of relieving the female partner and hatching and fledging success?; (iii) does clutch or brood size influence paternal care and mate-attraction effort?; and (iv) does this opportunity for EPCs or polygyny influence the amount of paternal care? The first three questions were examined experimentally by manipulating clutch and brood sizes and nest-box availability, and by monitoring the male and female reproductive behaviours before and after manipulations.

2. MATERIAL AND METHODS

(a) *Study population and observations of focal pairs*

The starlings were studied at three colonies (52, 34 and 26 nest-boxes) at Vosbergen, near Groningen (The Netherlands) from 14 April to 30 June 1999 and from 17 March to 28 June 2001. The colonies were separated by at least 500 m. Each colony consisted of uniform nest-boxes, situated *ca.* 6 m apart at a height of 2.5 m. During incubation, most males and females were colour marked and, during the nestling phase, the remainder were captured and colour marked. We observed all breeding pairs during the entire breeding cycle (1999: 47 pairs; 2001: 31 pairs) to quantify reproductive behaviour and male mating status (monogamous or polygynous). The nest-boxes were checked daily between 07.00 and 10.00 for the presence of eggs and start of incubation (determined by sensing the egg temperature). For each egg within a clutch, the laying date, and, if hatched, the hatching date, were determined by numbering the eggs with indelible ink. Intraspecific brood parasitism (the presence in a nest of two or more new eggs in one day; Yom-Tov 1980) was not observed in our population. Observations on incubation and

nestling provisioning were related to the start of incubation (i-day 0) and to hatching of the first egg (h-day 0), respectively. All nests with a clutch were monitored at i-day 5 for 90 min between 10.00 and 13.00, the time window when males perform most singing to obtain a secondary mate or EPCs (Pinxten & Eens 1997, 1998; Smith 1995). Telescopes, situated 50–60 m away from the focal box, allowed proper detection and identification of individuals as they arrived at and departed from their nest. When birds were not colour marked, the sexes were distinguished by bill coloration and plumage characteristics of breast and abdomen (Feare 1984). For each sex, we measured incubation attendance (proportion of time spent in the nest-box) and recesses (proportion of time spent outside nest-box). Ambient temperature was also recorded during each incubation watch, because temperature has previously been shown to affect male and female contributions to incubation (Smith *et al.* 1995). From i-day 12 until h-day 6, each clutch was checked three times daily (between 08.00 and 18.00) for hatching and for the presence of unhatched eggs. Nestlings were individually marked by clipping the nails of specific toes immediately after hatching, and were individually colour ringed between 8 and 11 days of age. All nests with broods were monitored at h-day 12 for 90 min between 10.00 and 13.00, following the same protocol as above. For each sex, we measured the frequency at which food was delivered to the young.

During each observation in 1999, we collected additional data for each focal male on their opportunities for polygyny and EPCs. Given that most polygynous males hold secondary females in the closest neighbouring nest-box (63.2%, $n = 19$ (Pinxten *et al.* 1989); 77.5%, $n = 40$ (Smith *et al.* 1994); 71.0%, $n = 7$ (1999 data of this study)), we quantified the opportunity for polygyny by the availability of an empty nest-box on either side of the focal nest-box. If these nest-boxes were occupied, we evaluated whether these neighbouring females were fertile and hence provided the possibility for extra-pair matings. Females were considered to be fertile from 6 days before they laid their first egg until the day when they laid their penultimate egg (Arvidsson 1992; Möller 1994). In 2001, we manipulated the availability of empty nest-boxes (see next section).

(b) *Manipulation of nest-box availability and observations on mate-attraction effort*

For the analyses of a trade-off between parental care and attraction of a secondary mate, only breeding pairs were used that had an opportunity to attract an additional female. These are breeding pairs with one empty nest-box available within 2 m of the occupied nest-box. Among the 34 observed monogamous males during the 1999 season, only 10 males had one and 4 males had two empty neighbouring nest-boxes available. During the 2001 season, we increased this sample through manipulation of nest-box availability to give each of the 31 monogamous males an equal opportunity to attract an additional female. On i-day 1, we removed all nest-boxes within a radius of 8 m from the focal nest-box and provided the focal male with one extra nest-box. The new nest-box was placed within 1.5–2 m of the original one, i.e. within the territory already defended by the male to avoid affecting the cost of defending nest-boxes (Smith 1995). During all incubation watches of these males (14 in 1999 and 31 in 2001) and food-provisioning watches (12 watches in 1999 and 24 in 2001), we monitored the focal male's (always colour ringed) efforts to attract secondary females and gain EPCs. These observations were conducted by two observers simultaneously; one observed the nest-box and the other the

focal male. The focal male's effort to attract an additional mate was scored as the duration of singing with 'wing-waving' within 2 m of the empty nest-box (hereafter termed 'nest-box singing') and the frequency of carrying green material into the nest-box. The focal male's effort to obtain EPCs was scored as the duration of singing high up in the trees within 5 m of a non-mate female (hereafter termed 'EPC singing').

(c) *Clutch-size manipulations*

Twelve sets of three monogamous pairs were selected (four in 1999 and eight in 2001) that had laid clutches of the same size (either five or six eggs) on the same date and had one empty nest-box within 2 m of their own nest-box. At all nests, incubation attendance of both sexes was measured on i-day 5 for 90 min between 10.00 and 13.00. Each of the three pairs of observers present was randomly assigned a nest-box. Within each set, on i-day 5 (half way through the incubation period of 12 days) between 14.00 and 16.30, one clutch was enlarged by three eggs, one was reduced by three eggs and one remained at the same size (control). Experimental and control treatments were randomly assigned to nest-boxes. To control for potential effects of foster-egg appearance on discrimination abilities of starlings, all nests, including controls, had similar fractions of new eggs. The manipulations within each set were always conducted by one person, keeping the other observers ignorant of the manipulation treatment. The manipulated nests were observed again on i-day 6 for 90 min between 10.00 and 13.00. Of each pair within each set, mate-attraction and EPC effort of the focal male and the amount of fresh green nesting material in the neighbouring nest-box (for methods, see previous section), were monitored during the observation periods before and after clutch manipulations. At i-day 11 (1 to 2 days before hatching), the exchanged eggs were returned to their original clutch, thus recreating the original clutch sizes.

(d) *Brood-size manipulations*

Nine sets of three monogamous pairs were selected (four sets in 1999 and five sets in 2001) that had broods of the same size (either five or six nestlings) of which the first young hatched on the same day and had one empty nest-box within 2 m of their own nest-box. All nests were monitored and manipulated at h-day 12 (half way through the nestling period of 20 days) and monitored again on h-day 13. For observations and manipulations, we used the same protocol and the same observation hours as described in the previous section. We measured the number of feeding visits for each sex, mate-attraction effort and EPC effort of the focal male (for methods, see above).

(e) *Data analyses*

Each pair produced only one clutch and observations in 1999 and 2001 involved different pairs to avoid duplications. For each pair, the laying date of the first egg was related to the date when the first egg in the colony was laid in that year (laying date 1). Total incubation attendance is expressed as the sum of attendance by both parents. The male's relative contribution to either incubation or food provisioning is expressed as his contribution to total incubation or total food provisioning, respectively. For either sex, the change in incubation attendance was calculated as the attendance at i-day 6 minus attendance at i-day 5, the change in food-provisioning rate as provisioning rate at h-day 13 minus provisioning rate at h-day 12, and in both cases corrected for the change in incubation attendance and food-provisioning rate at the control clutch or brood. For males, the

change in mate-attraction effort (nest-box singing duration and frequency of carrying green material) and EPC effort (EPC singing duration) were calculated in the same way. Because most variables deviated from normality, we used non-parametric statistics for most of our analyses, but we describe the data with least-squares linear fits. All parametric analyses were based on arcsine-transformed data. The relation between male nest-box singing and carrying frequency of green material on the one hand, and the acquisition of a secondary mate on the other hand, were analysed by stepwise forward logistic regression. A variable enters into the equation only if the probability (p) associated with the G -test on the decrease in scaled deviance (D') is less than 0.05. Means are expressed with standard errors, probability values are two-tailed and the null hypothesis was rejected at $p < 0.05$. Statistical analyses were performed using SPSS (version 10.0), and MLWIN (version 1.10, Rasbash *et al.* 2000) was used for binomial hierarchical models with nested data (for the analyses of hatching and fledging success). In the latter cases, t -tests were performed using the parameter estimate with its standard error and the degrees of freedom calculated from the number of cases at the nest level (i.e. the number of nests) minus the number of estimated parameters.

3. RESULTS

(a) *Trade-off between incubation attendance and singing activity*

(i) *Effect of clutch size*

The clutch sizes of observed nests varied from four to seven eggs, with a mean of 5.4 ± 0.9 ($n = 65$). Commonest clutch sizes were five (43.0%) and six (34.0%). Male incubation attendance and total incubation attendance increased significantly with clutch size, whereas female incubation attendance decreased with clutch size (figure 1a). The relative contribution to incubation by the male increased significantly with clutch size (figure 1a). Although male and female incubation attendances were inversely correlated, the female does not fully compensate for reduced paternal incubation (figure 1a). Male and female incubation attendance were independent of year, date and temperature during the incubation observation (general linear model: male: $F_{1,61} = 0.016$, $p = 0.90$, $F_{1,61} = 2.70$, $p = 0.11$ and $F_{1,61} = 0.19$, $p = 0.66$, respectively; female: $F_{1,61} = 0.037$, $p = 0.85$, $F_{1,61} = 0.55$, $p = 0.46$ and $F_{1,61} = 0.086$, $p = 0.77$, respectively; relative male incubation attendance: $F_{1,61} = 0.002$, $p = 0.97$, $F_{1,61} = 2.76$, $p = 0.10$ and $F_{1,61} = 0.58$, $p = 0.45$, respectively). Of the 41 clutches, which remained constant in size during the entire incubation period (65 clutches – 24 size-manipulated clutches = 41 clutches), male contribution to incubation explained most of the variance in hatching success (binomial hierarchical linear model; male incubation: $t = 4.27$, d.f. = 39, $p < 0.001$). A decreased male contribution to incubation of clutches was associated with the likelihood of hatching failure. After controlling for male incubation attendance, female incubation attendance and clutch size had no effect on hatchability (female incubation: $t = 0.73$, d.f. = 37, $p = 0.472$; clutch size: $t = 1.51$, d.f. = 37, $p = 0.139$). Given this important role of male incubation for hatching success, males with larger clutches may be expected to allocate more time to incubating the clutch and less time to attracting additional mates or pursuing EPCs.

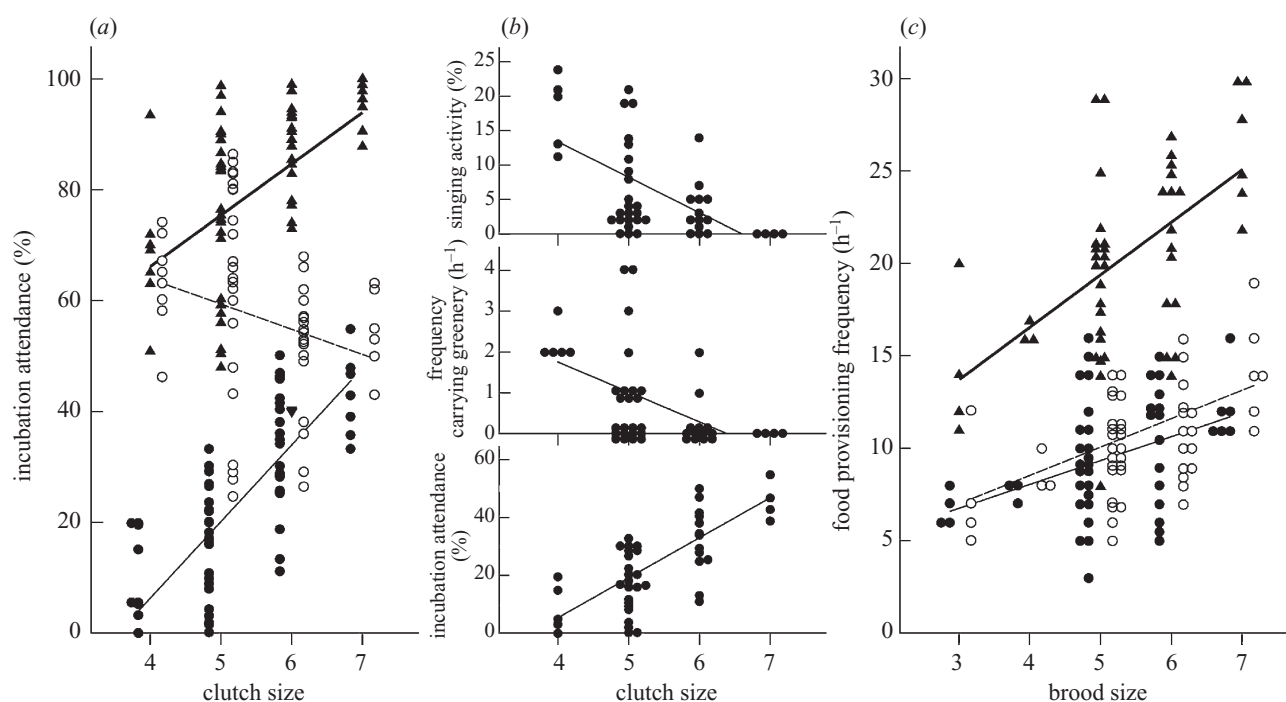


Figure 1. (a) Incubation attendance at day 5 of incubation (*y*-axis) in relation to natural clutch size (*x*-axis) by monogamous male and female starlings (male: $y = 13.84x - 51.32$; $r^2 = 0.56$, $n = 65$, $p < 0.001$; female: $y = -4.47x + 80.79$; $r^2 = 0.06$, $n = 65$, $p = 0.048$; total: $y = 9.28x + 29.01$; $r^2 = 0.22$, $n = 65$, $p < 0.001$). The relative contribution to incubation of the male (*y*) increased significantly with clutch size ($y = 0.13x - 0.44$; $r^2 = 0.43$, $n = 65$, $p < 0.001$). (b) Nest-box singing activity, frequency of carrying greenery into the empty nest-box and incubation attendance (*y*-axis) of the same males at day 5 of incubation in relation to natural clutch size (*x*-axis) (nest-box singing: $y = -5.13x + 33.84$; $r^2 = 0.35$, $n = 45$, $p < 0.001$; green carrying: $y = -0.73x + 4.68$; $r^2 = 0.27$, $n = 45$, $p = 0.009$; incubation: $y = 13.83x - 50.08$; $r^2 = 0.57$, $n = 45$, $p < 0.001$). (c) Food-provisioning frequency by monogamous male and female starlings on day 12 after hatching of the first egg (*y*-axis) in relation to natural brood size (*x*-axis) (male: $y = 1.30x + 2.80$; $r^2 = 0.18$, $n = 52$, $p = 0.002$; female: $y = 1.55x + 2.30$; $r^2 = 0.28$, $n = 52$, $p < 0.001$; total: $y = 2.84x + 5.10$; $r^2 = 0.69$, $n = 52$, $p < 0.001$). The relative contribution to food provisioning of the male was independent of brood size ($r^2 = 0.01$, $n = 52$, $p = 0.976$). Black circles, males; open circles, females; black triangles, total numbers. Thick regression line, total male and female provisioning; thin regression line, male provisioning; dashed regression line, female provisioning.

Considering only those males with at least one empty nest-box within 2 m of their own nest-box, there are two lines of evidence for a trade-off between incubation attendance and attraction effort of an additional mate. The larger the clutch, the more time spent incubating and the less time spent singing near the empty neighbouring nest-box, and the lower the frequency of carrying green nesting material into the empty nest-box by the focal male (figure 1b). Three of the four males that had two empty nest-boxes within 2 m of their own nest-box tried to attract an additional partner and always used the same empty nest-box (the other empty nest-box was not used). Hence, these four males are henceforward classified as males with one empty nest-box. Within individual males, the average amount of singing time near the empty nest-box was significantly higher than the average amount of singing time to obtain EPCs (mean nest-box singing: $6.3 \pm 1.1\%$; mean EPC singing: $1.9 \pm 0.4\%$; Wilcoxon paired-sample test: $Z = -3.72$, $n = 45$, $p < 0.001$). The male's EPC singing effort was independent of clutch size ($r^2 = 0.04$, $n = 45$, $p = 0.214$). Of the 21 males on which singing observations were conducted and whose clutches remained constant in size during the entire incubation period (45 males with singing observations – 24 males with size-manipulated clutches = 21 males), five males had acquired a secondary female (all in the neighbouring nest-

box) during the incubation period of the primary female (males were seen attending both nests). Both the amount of time spent singing near the empty nest-box and the carrying frequency of green nesting material by these males were positively associated with the chance of becoming polygynous at a later stage (nest-box singing explained most of the variance: $D = 11.81$, d.f. = 1, $n = 21$, $p = 0.001$; carrying greenery (controlled for nest-box singing): $D = 5.95$, d.f. = 1, $n = 21$, $p = 0.015$). The experimental clutch-size manipulations confirmed the plasticity of this trade-off within individual males. One day after the experimental reduction of clutch size, male incubation attendance had decreased and both nest-box singing activity and carrying frequency of greenery had increased significantly compared with the day before, and vice versa for males of experimentally increased clutch sizes (figures 2a and 3). By contrast, incubation attendance, singing activity and carrying frequency of greenery of control males remained the same during corresponding periods (figure 2a). The larger the decrease in incubation attendance, the more pronounced the increases in both singing time near the empty nest-box and carrying frequency of green nesting material into the empty nest-box, by the focal male (figure 2a). Males with control or enlarged clutches remained monogamous throughout the breeding season, whereas 33.0% of males with reduced

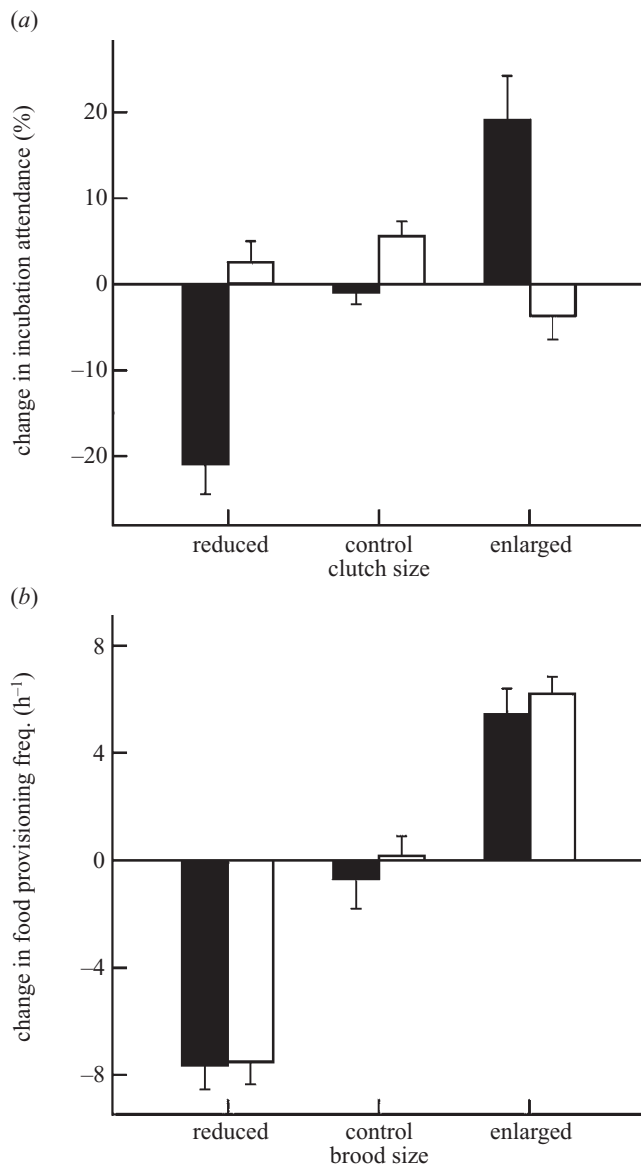


Figure 2. (a) The influence of clutch-size manipulations on change in percentage incubation attendance time within individual male and female starlings (male: $Z = 3.06$, $n = 12$ sets, $p = 0.002$; female: $Z = 1.25$, $n = 12$ sets, $p = 0.209$). One day after the experimental reduction or enlargement of clutch sizes, the change in male incubation attendance (y) was inversely associated with the change in female incubation attendance (x) ($y = -1.27x - 2.19$; $r^2 = 0.23$, $n = 24$, $p = 0.019$). (b) The influence of brood-size manipulations on change in food-provisioning rate within individual male and female starlings (male: $Z = 2.67$, $n = 9$ sets, $p = 0.008$; female: $Z = 2.68$, $n = 9$ sets, $p = 0.007$). One day after the experimental reduction or enlargement of brood sizes, male food-provisioning rate had changed to the same extent as female food-provisioning rate compared with the day before ($y = 0.93x - 0.47$; $r^2 = 0.88$, $n = 24$, $p < 0.001$). For the analyses of (a) and (b) only those males were included which had one empty nest-box within 2 m of their own nest-box. Black bars represent males and open bars represent females.

clutches had attracted an additional female into their empty neighbouring nest-box during the incubation period of their first female. This difference in the chance of becoming polygynous was significant (Kendall's W -test: $\chi^2 = 8.00$, d.f. = 2, $n = 13$ sets, $p = 0.018$). In contrast to

male incubation, clutch-size manipulations had no effect on female incubation attendance (figure 2a). However, one day after the experimental reduction of clutch sizes, a decrease in male incubation attendance was associated with an increase in female incubation attendance, and vice versa for enlargement of clutch sizes (figure 2a).

(ii) Effect of opportunity for polygyny

The investment in incubation attendance of the male was significantly associated with his opportunity for polygyny. Male incubation attendance (controlled for the effect of clutch size) was negatively related to the number of empty neighbouring nest-boxes on either side of the focal nest-box (figure 4), but unrelated to the number of fertile females in neighbouring nest-boxes of the focal nest-box ($F_{2,32} = 1.14$, $p = 0.335$).

(b) Brood size and trade-off between food provisioning and singing activity

The brood sizes of monogamous breeding pairs varied from three to seven nestlings, with a mean of 5.3 ± 0.1 ($n = 52$). The commonest brood sizes were five (46.0%) and six (29.0%). Across broods, the food-provisioning rate of both male and female increased significantly with brood size (figure 1c). However, the relative contribution to food provisioning of the male was independent of brood size (figure 1c). In addition, mean total food provisioning per nestling decreased significantly with brood size ($r^2 = -0.09$, $n = 52$, $p = 0.028$). Of the 34 broods, which remained constant in size during the entire nestling period (52 broods – 18 size-manipulated broods), the rate of food provisioning by either parent, controlling for brood size, had no effect on fledging success (binomial hierarchical linear model; male feeding: $t = 0.30$, d.f. = 31, $p = 0.766$; female feeding: $t = 0.17$, d.f. = 31, $p = 0.868$; brood size in both cases: $t > 0.51$, d.f. = 31, $p > 0.603$).

Considering only monogamous males with one empty nest-box within 2 m of their own nest-box, there was no evidence for the existence of a trade-off between food-provisioning rate and mate attraction effort by the male. First, males were never observed singing near the empty nest-box during the observations on food provisioning ($n = 52$). Second, these males were never observed carrying green nesting material into the empty nest-box. Third, one day after the experimental reduction of brood size, both male and female food-provisioning rate had decreased to the same extent compared with the day before, and, vice versa, for experimentally enlarged broods (figure 3b). During this period, unpaired and fertile females were absent from the colonies.

4. DISCUSSION

(a) Parental care in relation to clutch or brood size

In species with uniparental incubation, there is some evidence that larger clutches are perceived as more valuable. In Wilson's phalaropes (*Phalaropus tricolor*) with uniparental incubation, males are more likely to abandon experimentally reduced clutches (Delehanty & Oring 1993), while female European barn swallows (*Hirundo rustica*) increased attendance to experimentally enlarged clutches (Jones 1987). In species with biparental incu-

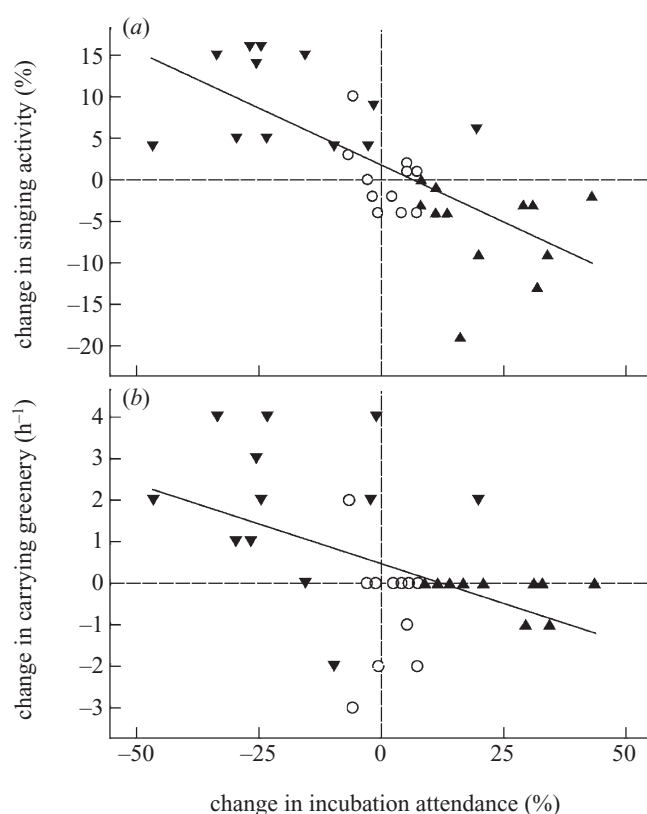


Figure 3. (a) The influence of clutch-size manipulations on change in percentage incubation attendance time (x-axis) and changes in percentage nest-box singing time (y-axis) within individual male starlings (nest-box singing: $y = -0.28x - 1.61$; $r^2 = 0.50$, $n = 36$, $p < 0.001$; $Z = 3.07$, $n = 12$ sets, $p = 0.002$). (b) The influence of clutch-size manipulations on change in percentage incubation attendance time (x-axis) and carrying greenery (y-axis) within individual male starlings (green carrying: $y = -3.8 \times 10^{-2}x + 0.44$; $r^2 = 0.22$, $n = 36$, $p = 0.004$; $Z = -2.58$, $n = 12$ sets, $p = 0.010$). For the analyses of (a) and (b) the same males were included, all of which had one empty nest-box within 2 m of their own nest-box. Black 'down' triangles represent reduced clutch size; open circles represent control clutch size; and filled 'up' triangles represent enlarged clutch size.

bation, there are only two studies that have considered male incubation in relation to clutch size. In the fairy martin, with fertile females present, male incubation attendance was positively associated with clutch size (Magrath & Elgar 1997). However, in captive-breeding zebra finches (*Taeniopygia guttata*), male incubation was independent of clutch size (Delesalle 1986), but this could be due to the fact that males had no access to other fertile females because pairs were isolated physically and visually, in cages. In the starling, male incubation attendance increased markedly in relation to clutch size, while female incubation declined. However, the observed increase in male contribution to larger clutches could also be explained by several other factors, other than the greater reproductive value of the clutch *per se*. (i) Elevated energetic costs of incubating a larger clutch (reviewed by Thomson *et al.* 1998), causing the male to perform a greater share of incubation to relieve the female. An increase in the metabolic cost of incubating larger clutches has been shown for the starling (Biebach 1984) and sev-

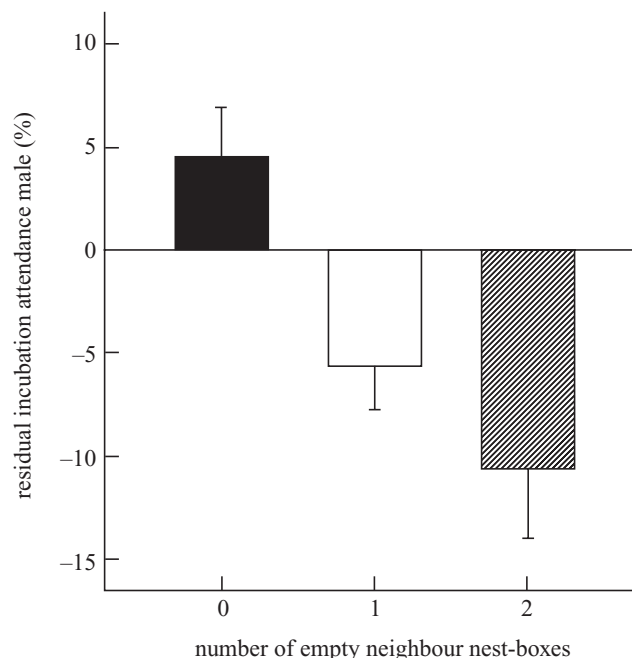


Figure 4. The association between polygyny potential and residual male incubation attendance (controlled for clutch size) at day 5 of incubation during the 1999 breeding season (polygyny potential expressed as the presence of 0–2 empty neighbour nest-boxes on either side of the focal nest-box; $F_{2,32} = 7.59$, $p = 0.002$). Black bar, $n = 20$; open bar, $n = 10$; hatched bar, $n = 4$.

eral other species (e.g. blue tit (*Parus caeruleus*), Haftorn & Reinertsen (1985); great tit (*Parus major*), Mertens (1977); zebra finch, Vleck (1981); Bengalese finch (*Lonchura striata*), Coleman & Whittall (1988)). These studies indicate that the cost of additional eggs is greatest at low ambient temperature. If metabolic cost is an important consideration, and given that in our study female incubation attendance decreased with clutch size, then relative male incubation attendance should increase with declining ambient temperature as the energetic cost of incubation increases. However this was not the case. (ii) Assortative pairing, in which males paired to females that produce larger clutches are of higher quality, contributing more to paternal care (e.g. moorhen (*Gallinula chloropus*); Petrie (1983)). However, in our study population, the relative male contribution declined with experimentally reduced clutch size, refuting the effect of assortative pairing on male incubation attendance. (iii) The production of eggs has been shown to be costly, which may affect parental care (Carey 1996). The production of a larger clutch may affect female condition, thus females are more likely to decrease incubation to regain energy losses (Carey 1996) and the males are responding to this reduction by increasing their investment (Smith & Härdling 2000). Although our clutch-size manipulation experiments demonstrated that the change in female incubation attendance was inversely associated with the change in male incubation attendance (figure 2a), this cannot be caused by differential female production costs. In our experiment, we compared similar initial clutch sizes of presumed similar production costs.

In a range of biparental species, relative male contribution to nestling feeding varies with brood size. Some

studies show that relative male contribution increases with brood size (Grundel 1987; Westneat 1988; Wright & Cuthill 1990; Carey 1990; Sanz 1997), others reported no change in relative contribution (Breithwisch *et al.* 1986; Leffelaar & Robertson 1986; Jones 1987; Moreno 1987; Smith *et al.* 1988; Verhulst & Tinbergen 1997) and, in a few species, relative male contribution declines with brood size (Hegner & Wingfield 1987; Buitron 1988). In contrast to the male starling's relative incubation attendance, the male's relative contribution to nestling feeding in our data was independent of brood size, suggesting that the reproductive value of the brood was similar for the male and female of pairs (see also next section).

(b) Clutch size and sexual conflict

Since clutch size is a female trait, because a male has little opportunity of influencing clutch size directly, this trait will evolve to the optimum value of females. However, the optimal clutch size from a female's perspective will depend on the amount of paternal care that she expects her mate to provide. The sexual conflict over parental care will, in turn, be affected by clutch or brood size, since a larger clutch or brood makes male parents more valuable in species with biparental care (Smith & Härdling 2000). However, so far it has been difficult to deduce whether the amount of paternal care is affected by a trade-off between attracting additional mates and the importance of male care for the fitness of primary clutches or broods. Evidence for a trade-off between male incubation and mate attraction comes from only two studies (empirical evidence: fairy martin, Magrath & Elgar (1997); experimental evidence: European starling, Smith (1995)). Our study is, to our knowledge, the first to offer an experimental demonstration and quantification that clutch size affects the amount of parental care and mate attraction effort in males (see also Westneat 1988; Westneat *et al.* 1990; Wright & Cuthill 1990; Whittingham 1993; Magrath & Elgar 1997). (i) We showed that the amount of time that males spent incubating was inversely related to singing activity near the empty nest-box, carrying frequency of green nesting material into the empty nest-box (figure 1b) and the chance of becoming polygynous. The amount of incubation had no effect on male singing time to obtain EPCs. (ii) Reduction of clutch size resulted in males spending significantly more time singing near the empty nest-box and carrying greenery than males in the control group (and vice versa for males that had clutches enlarged; figure 2a). Clutch-size manipulation also influenced the chances of males becoming polygynous. (iii) We found that the greater the reduction in male incubation attendance in the experimental group, the larger the increase in nest-box singing activity and carrying frequency of greenery (and vice versa for males that increased incubation attendance) (figure 3). However, there is no evidence for the existence of a trade-off between male care for nestlings and mate-attraction effort. This is, perhaps, unsurprising because unpaired and fertile females were absent during the nestling period.

Males should only be expected to allocate less time to attracting additional mates or pursuing EPCs if there is a cost to reduced male participation in incubation (Smith & Härdling 2000). In starlings, there is a cost of lower male attendance of the clutch because (i) there is incomplete

compensation in incubation effort between males and females. Females do not fully compensate for experimentally reduced male assistance (Wright & Cuthill 1989; Pinxten *et al.* 1993; this study; figure 2a); and (ii) reduced male contribution to incubation (controlled for clutch size) significantly increases the likelihood of hatching failure. This study concludes that, at the proximate level, the resolution of the trade-off between paternal care and mate-attraction effort is adjusted to clutch size. This study has shown that a trade-off between paternal and mate-attraction effort is the main explanation for the increase in male contribution to incubation with clutch size. We expect that similar clutch-size-related sex differences in parental care patterns occur in any species that exhibit biparental care and that are known to exhibit EPFs or facultative polygyny.

We thank F. H. Klein and J. Palsma for permission to work in the Vosbergen. We thank the following persons for their invaluable help in the field: Geerten Hengeveld, Menno Bouma, Liesbeth Feddema, Oscar Vedder, Ralph Mullers, Jörg Barke and Thijs van Overveld. We are grateful to Henrik Smith (Lund University, Sweden), Rudi Drent, Joost Tinbergen and Mathew Berg (Groningen University) and two anonymous referees for valuable comments that significantly improved the manuscript.

REFERENCES

- Arvidsson, B. L. 1992 Copulations and mate guarding in the willow warbler. *Anim. Behav.* **43**, 501–509.
- Beecher, M. D. & Beecher, I. M. 1979 Sociobiology of the bank swallows: reproductive strategy of the male. *Science* **205**, 1282–1285.
- Biebach, H. 1984 Effect of clutch size and time of day on the energy expenditure of incubating starlings, *Sturnus vulgaris*. *Physiol. Zool.* **57**, 26–31.
- Birkhead, T. R. & Möller, A. P. 1992 *Sperm competition in birds: evolutionary causes and consequences*. London: Academic.
- Birkhead, T. R., Burke, T., Zann, R., Hunter, F. M. & Krupa, A. P. 1990 Extra-pair paternity and intra-specific brood parasitism in wild zebra finches *Taeniopygia guttata* revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.* **27**, 316–324.
- Breihagen, T. & Slagsvold, T. 1988 Male polyterritoriality and female–female aggression in the pied flycatcher *Ficedula hypoleuca*. *Anim. Behav.* **36**, 604–606.
- Breithwisch, R., Meritt, P. G. & Whitesides, G. H. 1986 Parental investment by the northern mockingbird: male and female roles in feeding nestlings. *Auk* **103**, 152–159.
- Bruun, M., Sandell, M. I. & Smith, H. G. 1997 Polygynous male starlings allocate parental care effort according to relative hatching date. *Anim. Behav.* **54**, 73–79.
- Buitron, D. 1988 Female and male specialization in parental care and its consequences in black-billed magpies. *Condor* **90**, 29–39.
- Carey, M. 1990 Effects of brood size and nestling age on parental care by male field sparrows, *Spizella pusilla*. *Auk* **107**, 580–586.
- Carey, C. 1996 Female reproductive success. In *Avian energetics and nutritional ecology* (ed. C. Carey), pp. 324–376. New York: Chapman & Hall.
- Clutton-Brock, T. 1991 *The evolution of parental care*. Princeton University Press.
- Coleman, R. M. & Whittall, R. D. 1988 Clutch size and the cost of incubation in the Bengalese finch, *Lonchura striata* var. *domestica*. *Behav. Ecol. Sociobiol.* **23**, 367–372.
- Cucco, M. & Malacarne, G. 1997 The effect of supplemental

- food on time budget and body condition in the black redstart *Phoenicurus ochruros*. *Ardea* **85**, 211–221.
- Cuthill, I. C. & Hindmarsh, A. 1985 Increase in starling song activity with removal of mate. *Anim. Behav.* **33**, 326–328.
- Delehanty, D. J. & Oring, L. W. 1993 Effect of clutch size on incubation persistence in male Wilson's phalaropes (*Phalaropus tricolor*). *Auk* **110**, 521–528.
- Delesalle, V. A. 1986 Division of parental care and reproductive success in the zebra finch, *Taeniopygia guttata*. *Behav. Process.* **12**, 1–22.
- Dixon, A., Ross, D., O'Malley, S. L. C. & Burke, T. 1994 Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* **371**, 698–700.
- Dunn, P. O. & Hannon, S. J. 1991 Intraspecific competition and the maintenance of monogamy in tree swallows. *Behav. Ecol.* **2**, 258–266.
- Eens, M. & Pinxten, R. 1990 Extra-pair courtship in the European starling. *Ibis* **132**, 618–619.
- Eens, M., Pinxten, R. & Verheyen, R. F. 1990 On the function of singing and wing-waving in the European starling *Sturnus vulgaris*. *Bird Study* **37**, 48–52.
- Eens, M., Pinxten, R. & Verheyen, R. F. 1991 Male song as a cue for mate choice in the European starling. *Behaviour* **116**, 210–238.
- Eens, M., Pinxten, R. & Verheyen, R. F. 1993 Function of the song and song repertoire in the European starling (*Sturnus vulgaris*): an aviary experiment. *Behaviour* **125**, 51–65.
- Emlen, S. T. & Oring, L. W. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.
- Feare, C. J. 1984 *The starling*. Oxford University Press.
- Gibbs, H. L., Weatherhead, P. J., Boag, P. T., White, B. N., Tabak, L. M. & Hoysak, D. J. 1990 Realized reproductive success of polygynous red-winged black birds revealed by DNA markers. *Science* **250**, 1394–1397.
- Grundel, R. 1987 Determinants of the nestling feeding rates and parental investment in mountain chickadees. *Condor* **89**, 319–328.
- Gwinner, H. 1997 The function of green plants in nests of European starlings (*Sturnus vulgaris*). *Behaviour* **134**, 337–351.
- Haftorn, S. & Reinertsen, R. E. 1985 The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit, *Parus caeruleus*. *Auk* **102**, 470–478.
- Hannon, S. J. 1984 Factors limiting polygyny in the willow ptarmigan. *Anim. Behav.* **32**, 153–161.
- Hegner, A. I. & Wingfield, J. C. 1987 Effects of brood size manipulation on parental investment, breeding success, and reproductive endocrinology of house sparrows. *Auk* **104**, 470–480.
- Jones, G. 1987 Time and energy constraints during incubation in free-living swallows, *Hirundo rustica*: an experimental study using precision electronic balances. *J. Anim. Ecol.* **56**, 229–245.
- Kempnaers, B. 1994 Polygyny in the blue tit: unbalanced sex ratio and female aggression restrict mate choice. *Anim. Behav.* **47**, 943–957.
- Kempnaers, B., Verheyen, G. R., Van den Broeck, M., Burke, T., Van Broeckhoven, C. & Dhondt, A. A. 1992 Extra-pair paternity results from female preference for high-quality males in blue tit. *Nature* **357**, 494–496.
- Leffelaar, D. & Robertson, R. J. 1986 Equality of feeding roles and the maintenance of monogamy in tree swallows. *Behav. Ecol. Sociobiol.* **18**, 199–206.
- Magrath, M. J. L. & Elgar, M. A. 1997 Paternal care declines with increased opportunity for extra-pair matings in fairy martins. *Proc. R. Soc. Lond. B* **264**, 1731–1736. (DOI 10.1098/rspb.1997.0240.)
- Maynard Smith, J. 1978 *The evolution of sex*. Cambridge University Press.
- Merkel, F. W. 1978 Sozial Verhalten von individuell markierten Staren (*Sturnus vulgaris*) in einer kleinen Nistkastenkolonie (1. Mitteilung)—Gruppenbild um einem Staren-Mann. *Luscinia* **43**, 163–186.
- Mertens, J. A. L. 1977 The energy requirements for incubation in great tits, *Parus major* L. *Ardea* **65**, 184–196.
- Moreno, J. 1987 Parental care in the wheatear, *Oenanthe oenanthe*, effects of nestling age and brood size. *Ornis Scand.* **18**, 291–301.
- Mountjoy, D. J. & Lemon, R. E. 1991 Song as an attractant for male and female European starlings, and the influence of song complexity on their response. *Behav. Ecol. Sociobiol.* **28**, 97–100.
- Møller, A. P. 1994 *Sexual selection and the barn swallow*. New York: Oxford University Press.
- Orians, G. H. 1969 On the evolution of mating systems in birds and mammals. *Am. Nat.* **103**, 589–603.
- Patterson, C. B., Erckmann, W. J. & Orians, G. H. 1980 An experimental study of parental investment and polygyny in male blackbirds. *Am. Nat.* **116**, 757–769.
- Petrie, M. 1983 Female moorhens compete for small fat males. *Science* **220**, 413–414.
- Pinxten, R. & Eens, M. 1994 Male feeding of nestlings in the facultatively polygynous European starling: allocation patterns and effect on female reproductive success. *Behaviour* **129**, 113–140.
- Pinxten, R. & Eens, M. 1997 Copulation and mate-guarding patterns in polygynous European starlings. *Anim. Behav.* **54**, 45–58.
- Pinxten, R. & Eens, M. 1998 Male starlings sing most in the late morning, following egg-laying: a strategy to protect their paternity? *Behaviour* **135**, 1197–1211.
- Pinxten, R., Eens, M. & Verheyen, R. F. 1989 Polygyny in the European starling. *Behaviour* **111**, 234–256.
- Pinxten, R., Eens, M. & Verheyen, R. F. 1993 Male and female attendance during incubation in the facultatively polygynous European starling. *Ardea* **81**, 125–133.
- Rasbash, J., Browne, W., Goldstein, H., Yang, M., Plewis, I., Healy, M., Woodhouse, G., Draper, D., Langford, I. & Lewis, T. 2000 *A user's guide to MLWIN*, 2nd edn. London: Institute of Education.
- Sandell, M. I. & Smith, H. G. 1996 Already mated females constrain male mating success in the European starling. *Proc. R. Soc. Lond. B* **263**, 743–747.
- Sandell, M. I., Smith, H. G. & Bruun, M. 1996 Paternal care in European starling, *Sturnus vulgaris*: nestling feeding. *Behav. Ecol. Sociobiol.* **39**, 301–309.
- Sanz, J. S. 1997 Clutch size manipulation in the pied flycatcher: effects on nestling growth, parental care and moult. *J. Avian Biol.* **28**, 157–162.
- Searcy, W. A. & Yasukawa, K. 1989 Alternative models of territorial polygyny in birds. *Am. Nat.* **134**, 323–342.
- Slagsvold, T. & Lifjeld, J. T. 1994 Polygyny in birds: the role of competition between females for male parental care. *Am. Nat.* **143**, 59–94.
- Smith, H. G. 1995 Experimental demonstration of a trade-off between mate attraction and paternal care. *Proc. R. Soc. Lond. B* **260**, 45–51.
- Smith, H. G. & Härdling, R. 2000 Clutch size evolution under sexual conflict enhances the stability of mating systems. *Proc. R. Soc. Lond. B* **267**, 2163–2170. (DOI 10.1098/rspb.2000.1264.)
- Smith, H. G. & Sandell, M. I. 1998 Intersexual competition in a polygynous mating system. *Oikos* **83**, 484–495.
- Smith, H. G. & Von Schantz, T. 1993 Extra-pair paternity in the European starling: the effect of polygyny. *Condor* **95**, 1006–1015.
- Smith, H. G., Ottoson, U. & Sandell, M. 1994 Intra-sexual

- competition among polygynously mated female starlings (*Sturnus vulgaris*). *Behav. Ecol.* **5**, 57–63.
- Smith, H. G., Sandell, M. I. & Bruun, M. 1995 Parental care in the European starling, *Sturnus vulgaris*: incubation. *Anim. Behav.* **50**, 323–331.
- Smith, H. G., Källander, H., Fontell, K. & Ljungström, M. 1988 Feeding frequency and brood division labour in the double brooded great tit, *Parus major*. *Behav. Ecol. Sociobiol.* **22**, 447–453.
- Thomson, D. L., Monaghan, P. & Furness, R. W. 1998 The demands of incubation and avian clutch size. *Biol. Rev.* **73**, 293–304.
- Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man* (ed. B. Campbell), pp. 52–97. Chicago, IL: Aldine Publishing Co.
- Veiga, J. P. 1992 Why are house sparrows predominantly monogamous? A test of hypotheses. *Anim. Behav.* **43**, 361–370.
- Verhulst, S. & Tinbergen, J. M. 1997 Clutch size and parental effort in the great tit *Parus major*. *Ardea* **85**, 111–126.
- Vleck, C. M. 1981 Energetic cost of incubation in the zebra finch. *Condor* **83**, 229–237.
- Webster, M. S. 1991 Male parental care and polygyny in birds. *Am. Nat.* **137**, 274–280.
- Westneat, D. F. 1988 Male parental care and extra-pair copulations in the indigo bunting. *Auk* **105**, 149–160.
- Westneat, D. F. & Sargent, R. C. 1996 Sex and parenting: the effects of sexual conflict and parentage on parental strategies. *Trends Ecol. Evol.* **11**, 87–91.
- Westneat, D. F. & Sherman, P. W. 1993 Parentage and the evolution of parental behaviour. *Behav. Ecol.* **4**, 66–77.
- Westneat, D. F. & Webster, M. S. 1994 Molecular analysis of kinship in birds: interesting questions and useful techniques. In *Molecular ecology and evolution: approaches and applications* (ed. B. Schierwater, B. Streit, G. P. Wagner & R. DeSalle), pp. 91–126. Basel: Birkhäuser.
- Westneat, D. F., Sherman, P. W. & Morton, M. L. 1990 The ecology and evolution of extra-pair copulations in birds. *Curr. Ornithol.* **7**, 331–369.
- Wetton, J. H., Burke, T., Parkin, D. T. & Cairns, E. 1995 Single-locus DNA fingerprinting reveals that male reproductive success increases with age through extra-pair paternity in the house sparrow (*Passer domesticus*). *Proc. R. Soc. Lond. B* **260**, 91–98.
- Whittingham, L. A. 1993 Effects of nestling provisioning on the time-activity budgets of male red-winged blackbirds. *Condor* **95**, 730–734.
- Whittingham, L. A., Taylor, P. D. & Robertson, R. J. 1992 Confidence of paternity and male parental care: an experimental study in tree swallows. *Anim. Behav.* **46**, 139–147.
- Wright, J. & Cuthill, I. 1989 Manipulation of sex differences in parental care. *Behav. Ecol. Sociobiol.* **25**, 171–181.
- Wright, J. & Cuthill, I. 1990 Manipulation of sex differences in parental care: the effect of brood size. *Anim. Behav.* **40**, 462–471.
- Yasukawa, K. & Searcy, W. A. 1982 Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. *Behav. Ecol. Sociobiol.* **11**, 13–17.
- Yom-Tov, Y. 1980 Intraspecific nest parasitism in birds. *Biol. Rev.* **55**, 93–108.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.